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THE GENERA OF LEPIDIEAE
(CRUCIFERAE; BRASSICACEAE) IN THE
SOUTHEASTERN UNITED STATES^{1,2}

IHSAN A. AL-SHEHBAZ³

Tribe *Lepidieae* A. P. de Candolle, *Syst. Nat.* 2: 151. 1821.

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs], glabrous or with simple or rarely stellate [or bifurcate or dendritic] trichomes. Inflorescence an ebracteate [or bracteate], corymbose raceme, usually elongated in fruit; flowers few to many [rarely solitary on long scapes], actinomorphic or slightly [to strongly] zygomorphic, perfect [or very rarely imperfect and plants monoecious or dioecious]. Sepals erect to ascending or spreading, not saccate [or strongly saccate] at base. Petals present or absent, equal or unequal. Nectar glands 2, 4, or 6, distinct or connate, subtending [or surrounding] the bases of

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²For an account of the family and its tribes, see Al-Shehbaz, The tribes of Cruciferae (Brassicaceae) in the southeastern United States. *Jour. Arnold Arb.* 65: 343–373. 1984.

³Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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filaments. Stamens 2 or 6 [rarely 4 or 8–24], subequal or tetradynamous, with or without a basal appendage. Siliques usually less than 3 times [very rarely to 20 times] longer than broad, strongly [to slightly] flattened at right angles to the septum (angustiseptate) [or rarely inflated], dehiscent or indehiscent [sometimes modified into schizocarps or 1-seeded samaras], sessile [or rarely stipitate]; valves winged or wingless, thick [or membranaceous]; replum much narrower than [or rarely subequaling] the width of the fruit; septum present [or absent]; styles present or absent; stigmas entire [or 2-lobed]. Seeds 1 to several or numerous, mucilaginous or not when wet, wingless or narrowly [to broadly] winged; cotyledons accumbent or incumbent. (Including *Brachycarpaeae* DC., *Cremolobeae* Hayek, *Iberideae* Godron, *Isatideae* DC., *Senebieraeae* Godron, *Subularieae* DC., *Thlaspideae* DC.) TYPE GENUS: *Lepidium* L.

A natural tribe of about 66 genera (23 monotypic) and some 680 species distributed throughout the world, with the major center of diversification in the Irano-Turanian region, where some 26 genera (13 endemic) and 190 species are found. Other important centers are the Mediterranean region, with 15 genera (four endemic) and about 97 species, eastern and central Asia, with 17 genera (ten endemic) and some 87 species, South America, with ten genera (six endemic) and approximately 86 species, and North America, with 14 genera (eight endemic) and nearly 75 species. In Australia and New Zealand there are about 58 species and five endemic genera, while in Africa (excluding the Mediterranean part) only 25 indigenous species and one endemic genus are found. Nearly half of the species of the tribe belong to five genera: *Lepidium* (175), *Thlaspi* L. (75), *Aethionema* R. Br. (60), *Isatis* L. (60), and *Biscutella* L. (40). Only *Lepidium* is represented by indigenous species on all continents except Antarctica. The Lepidieae are represented in the southeastern United States by six genera and 17 species, of which all, except five of *Lepidium*, are naturalized European weeds. Three additional “wool-alien” lepidiums have recently been reported from waste grounds around wool-combing mills in South Carolina, but none has become established anywhere in the Southeast. *Dithyrea* Harvey was listed for Arkansas by Small (1903), but according to Rollins (1979), the genus does not occur in our area.

Although the Lepidieae are easily distinguished by the angustiseptate siliques (flattened perpendicular to the septum), which are generally less than three times longer than broad (FIGURE 1), the tribal boundaries are sometimes artificially drawn. In some genera the fruits are inflated or only weakly angustiseptate, while in others they are about 20 times longer than broad. Angustiseptate siliques have evolved independently several times within the Cruciferae, and examples outside the Lepidieae are found in *Psychine* Desf. (monotypic; northwestern Africa) and *Schouwia* DC. (two species; North Africa and Arabia), of the Brassiceae; *Lesquerella* S. Watson, of the Alyseae DC.; *Caulanthus californicus* (S. Watson) Payson, of the Thelypodieae Prantl; and *Smelowskia* C. A. Meyer, of the Sisymbrieae DC. The distinction between latiseptate (flattened parallel to the septum) and angustiseptate fruits is usually considered to be highly significant in the classification of the Cruciferae. Both types of fruits, however, occur within the North American members of *Lesquerella* and the

Irano-Turanian genus *Graellsia* Boiss. The latter was divided according to the type of fruit into two genera, each placed in a different tribe (Schulz, Poulter). Angustiseptate, latiseptate, and terete fruits of various lengths are found in *Nerisyrenia* Greene (nine species; North America) and in the North American species of *Smelowskia* (Bacon, Drury & Rollins). These genera cannot be assigned adequately to tribes on the basis of fruit characters and should therefore have the same tribal disposition as their nearest generic relatives. Schulz overemphasized the flattening of the siliques in defining the boundaries of the Lepidieae, and this led to some artificiality in his classification. For example, he maintained *Cardaria* Desv. in the Lepidieae and placed its congener *Hymenophysa* C. A. Meyer, which has globose fruits, in the Euclidieae DC. Similarly, he assigned *Sphaerocardamum* Schauer, with globose fruits, to the Sisymbrieae and proposed *Cibotarium* O. E. Schulz (Lepidieae) for species with angustiseptate fruits (see Rollins, 1984). In my opinion, *Cardaria* (including *Hymenophysa*) and *Sphaerocardamum* (including *Cibotarium*) should be retained in the Lepidieae.

The limits of the Lepidieae are expanded here to include the South American tribe Cremolobeae, which consists of *Cremolobus* DC. (seven species) and *Menonvillea* R. Br. ex DC. (29 species). The latter tribe is recognized by several authors (see Hedge, 1976) and is distinguished by the presence of a gynophore, the absence of a septum, the complete or partial union of the replum margins into a solid or fenestrate stalklike structure, the modification of the valves into one-seeded mericarps, and the frequent attachment of each mericarp to a filiform carpophore derived from the lateral ridges of the style. To those unfamiliar with the Cruciferae, such unusual schizocarpic fruits may justify the recognition of the Cremolobeae as a distinct tribe. Careful study of the entire tribe Lepidieae, however, reveals that several Old World genera, particularly *Biscutella* and *Megacarpaea* DC., have fruits similar to those of the Cremolobeae. I fully concur with De Candolle (1821, 1824) in maintaining the four above genera in the same tribe. Avetisian has recently merged the Cremolobeae with the Thelypodieae and the Lepidieae with the Sisymbrieae. In my opinion, the Lepidieae are a natural tribe that should include both *Cremolobus* and *Menonvillea*.

There is little agreement among various classifications as to the limits of the Lepidieae and the number and limits of its subtribes. The genera that I place in the Lepidieae were assigned to five tribes by Von Hayek and to seven by De Candolle (1821, 1824) and Bentham & Hooker. Four of the 12 subtribes recognized by Schulz are unigeneric and can be easily accommodated in some of the larger ones without drastically altering their limits. At least five of the remaining subtribes, Lepidiinae Prantl, Isatidinae Hayek (probably including *Horwoodia* Turrill), Cremolobinae Prantl (including most of the Iberidinae Hayek), Capsellinae Hayek, and Thlaspidinae Hayek, are sufficiently distinct and may merit recognition. Subtribe Physariinae Prantl and the genera *Lesquerella* and *Physaria* will be discussed in the treatment of tribe Alysseae DC. for the Generic Flora.

Autogamy is fairly common in the weedy members of the Lepidieae. In *Lepidium* and *Coronopus* Zinn it is often associated with either the modification



FIGURE 1. Selected representatives of tribe Lepidieae. a-f, *Capsella Bursa-pastoris*: a, plant with flowers and fruits, $\times \frac{1}{2}$; b, flower, $\times 12$; c, flower with sepal and 2 petals removed to show tetradynamous stamens, $\times 12$; d, fruit, $\times 3$; e, replum and septum,

of petals into bristles or their absence, the lack of scent and color, and the presence of only two stamens. Submersed plants of the circumpolar *Subularia aquatica* L. always produce cleistogamous flowers. Monoecism, dioecism, and polyandry, which are very rare in the Cruciferae, are known in only a few species of this tribe. Monoecism has been reported thus far only in *Megacarpaea megalocarpa* (Fischer ex DC.) Schischkin ex Fedtsch., of southeastern Russia and central Asia, while dioecism is known only in three New Zealandic species of *Lepidium*, which are reduced by some authors to subspecies of *L. sisymbrioides* Hooker f. Polyandry has been reported only in the Himalayan *Megacarpaea polyandra* Benthams, which has eight to 24 stamens. Flower color is variable in the tribe, but in *Brachycarpaea juncea* (Berg.) Marais, an endemic of the Cape Province of South Africa, it is described as white, pink, blue, violet, purple, and mauve.

Chromosome numbers are known for at least 260 species (ca. 40 percent of the tribe) and 35 genera. More than 35 percent of the taxa have a base chromosome number of seven, while about 25 percent are based on eight and approximately 15 percent on nine (author's compilation). The lowest chromosome number ($2n = 12$) is found in several species of *Cochlearia* L., while the highest ($2n = 128$) is found in *Cardaria Draba* (L.) Desv. subsp. *chalepensis* (L.) O. E. Schulz. About 67 percent of the species are diploid, and only 23 percent are exclusively polyploid. Polyploidy and aneuploidy probably played important roles in the evolution of *Aethionema*, *Biscutella*, *Cochlearia*, and *Nerisyrenia*.

The tribe has been poorly surveyed for chemical constituents. The seeds of only 22 species in nine genera have been analyzed for fatty-acid composition (Kumar & Tsunoda). The scant data show high concentrations of linolenic and eicosenoic acids and lower amounts or the absence of erucic acid in all but six species of *Thlaspi* and *Isatis*. About 40 species and 15 genera have been surveyed for glucosinolates (author's compilation and unpublished data). The dominant compounds appear to be benzylglucosinolate, its ring-oxidized methoxylated or hydroxylated relatives, and several methionine-derived glucosinolates. Only one genus, *Nerisyrenia*, has been thoroughly studied for flavonoids, which have been shown to be very helpful in suggesting species relationships and phyletic groupings, as well as in distinguishing between species (Bacon).

The tribe is almost exclusively herbaceous; only a few unrelated species are typical shrubs. In *Lepidium scandens* Hewson (Australia) and *Cremolobus peruvianus* (Lam.) DC. (Peru) the stems are reported to reach two and five meters, respectively. Both species are said to be vines, a habit unusual in the Cruciferae (Hewson, Khanna & Rollins).

× 3; f, seed, × 25. g, h, *Coronopus didymus*: g, portion of plant with fruits, × 2; h, fruit, × 6. i-l, *Lepidium virginicum*: i, portion of plant with fruits, × 1; j, fruit, × 6; k, seed, × 6; l, embryo (note accumbent cotyledons), × 6. m-o, *L. campestre*: m, fruit, × 6; n, fruit after fall of valve (note apical attachment of seed), × 6; o, embryo (note incumbent cotyledons), × 6. p-r, *Teesdalia nudicaulis*: p, fruit, × 6; q, fruit after removal of valve, × 6; r, seed, × 12. s-u, *Thlaspi arvense*: s, fruit, × 2; t, fruit after fall of valve and 3 seeds, × 2; u, seed (note striate testa), × 6.

Members of the Lepidieae with dehiscent fruits often have mucilaginous seeds, which upon wetting may be dispersed for long distances by adhering to animals. Dustlike or broadly winged seeds, which are uncommon in the tribe, may be dispersed by wind. The majority of indehiscent fruits contain one or two nonmucilaginous seeds, and in many species they are modified into samaras or schizocarpic samaras. Some become strongly inflated and are therefore adapted to dispersal by wind. Samaroid fruits must have evolved independently within the tribe, as evidenced by their occurrence in several unrelated genera. For example, the fruits of some species of *Isatis*, which may be easily confused with the samaras of *Fraxinus* L. (Oleaceae), are quite different from the remarkable fruits of *Pugionium* Gaertner (five species; Mongolia) that have various numbers of wings and appendages. Schulz placed both genera in the same subtribe, but they are clearly unrelated. These genera are also unrelated to either *Brossardia* Boiss. (monotypic; Iraq and Iran) or *Menonvillea*, which have one-winged papery samaras and two- to ten-winged schizocarpic samaras, respectively.

In some of the annual species of *Aethionema*, heterocarpic fruits (dehiscent with several mucilaginous seeds in each of the two locules and indehiscent with a nonmucilaginous seed in the single locule) are produced on the same infructescence. Heterocarpy is genetically fixed in *Aethionema* and is changed little or not at all by environmental conditions (Puech). Voytenko listed heterocarpy in 41 genera of the Cruciferae (including many members of the Brassiceae with segmented fruits), but it appears that only *Aethionema* typically exhibits this feature. In the heterocarpic species the indehiscent fruits differ from the dehiscent ones by the total disappearance of the septum during the early stages of development, the abortion of all but one of the four to many ovules, and the total lignification of the dehiscence line near the replum (Zohary & Fahn). The production of heterocarpic fruits may be an adaptation to different modes of dispersal in steppes and deserts, where most annual species of *Aethionema* occur.

The majority of the Lepidieae occupy mesic habitats, and only a few genera are typically hydrophytic (*Subularia* L.) or xerophytic (*Horwoodia*). In *S. aquatica*, which is usually completely submersed in shallow littoral lakes, the roots and leaves have a remarkably similar anatomy with extensive aerenchyma (Hiltner). The stomata are permanently open, and the guard cells are raised above the leaf surface. The species also grows occasionally as a stunted plant of wet ground, just as its Afro-alpine relative *S. monticola* Schweinf. (Woodhead) does.

Seed size in the tribe shows a very wide range of variation, and the largest and smallest seeds in the Cruciferae are found in *Megacarpaea* and *Mancoa* Weddell, respectively. In *Megacarpaea gigantea* Regel, an endemic of grassy mountain slopes in central Asia, the seeds are about 1.8 × 1.5 cm and may weigh more than 90 mg. Each seed is borne inside a large (4 × 3 cm), broadly winged mericarp. The dustlike seeds of *Mancoa mexicana* Gilg & Muschler, an endemic of the high plains in Jalisco and San Luis Potosí, Mexico, are about 0.3 mm long and weigh only about 0.02 mg (less than one forty-five-hundredth the seed weight of the former species).

The representatives of the Lepidieae in the southeastern United States either are cosmopolitan weeds or are potentially weedy. Some are serious competitors capable of reducing the yield of wheat, while others taint the dairy products obtained from cattle feeding on them. A few species are hosts for several fungi and viruses that attack various cruciferous crops. The young parts of some species are eaten as a salad, and *Lepidium sativum* L. is cultivated throughout the world for that purpose. Many species of *Iberis* L. (candytuft), *Aethionema* (stone cress), and *Thlaspi* (penny cress) are ornamentals grown in rock gardens or flower beds, and a few are used in ornamental dry arrangements. *Isatis tinctoria* L. was formerly grown for woad, a historically important blue dye obtained from its ground, fermented leaves.

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KEY TO THE GENERA OF LEPIDIEAE IN THE
SOUTHEASTERN UNITED STATES⁴

- A. Seeds 1 in each locule.
- B. Fruits coarsely reticulate or verrucose, often didymous; seeds not mucilaginous when wet; upper cauline leaves 1- or 2-pinnatisect; at least some inflorescences axillary. 15. *Coronopus*.
- B. Fruits smooth, not didymous; seeds mucilaginous when wet; upper cauline leaves entire, toothed, or rarely pinnatisect; inflorescences terminal.
- C. Fruits dehiscent, narrowly winged, retuse to emarginate at apex. 14. *Lepidium*.
- C. Fruits indehiscent, wingless, acute or obtuse at apex. 16. *Cardaria*.
- A. Seeds 2 or more in each locule.
- D. Fruits obcordate-triangular; plants with simple, furcate, and stellate trichomes. 19. *Capsella*.
- D. Fruits orbicular-obcordate; plants glabrous.
- E. Flowers zygomorphic; median filaments with broad, scalelike, basal appendage; seeds 2 per locule; basal leaves pinnatifid. 18. *Teesdalia*.
- E. Flowers actinomorphic; median filaments not appendaged; seeds 3 or more (rarely 2) per locule; basal leaves entire or dentate. 17. *Thlaspi*.

14. **Lepidium** Linnaeus, *Sp. Pl.* 2: 643. 1753; *Gen. Pl.* ed. 5. 291. 1754.

Annual, biennial [or perennial] herbs [rarely subshrubs or shrubs to 2 m high], glabrous, papillose, or with simple unicellular trichomes. Stems erect or ascending, sometimes procumbent [very rarely twining]. Basal leaves petiolate, entire to pinnately lobed or 1- to 3-pinnatisect, usually not forming a rosette. Cauline leaves short petiolate or sessile, sometimes auriculate or amplexicaul. Inflorescence an ebracteate, corymbose raceme, greatly [or slightly] elongated in fruit; flowers many, small, pedicellate, perfect [or very rarely imperfect and plants dioecious]. Sepals erect to spreading, not saccate at base, oblong or ovate [rarely orbicular], glabrous or pubescent, sometimes scarious at margin, caducous or persistent until [or after] fruit maturity. Petals oblanceolate, spatulate, obovate, linear, or filiform, sometimes reduced to bristles or absent, longer or shorter than the sepals, usually white, occasionally yellow, pink, or lavender; claws (when present) filiform [very rarely pseudotubular and with a cucullate nectar-accumulating base]. Nectar glands 4 or 6, ovate, triangular, or filiform, median pairs always present, lateral pair sometimes absent. Stamens

⁴The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (*Jour. Arnold Arb.* 65: 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* 66: 95–111. 1985, and genera 3–13 (Brassicaceae) in *ibid.* 279–351.

usually 2, less commonly 6 and slightly tetradynamous, occasionally 4; filaments linear or subulate, wingless, not appendaged, sometimes dilated at base; anthers oblong or ovoid. Ovary 2-ovulate; styles present or absent; stigmas capitate, entire [or slightly 2-lobed]. Fruiting pedicels terete or slightly [to strongly] flattened [or winged], divaricate to ascending [or erect]. Fruits dehiscent, as long as to twice as long as broad, strongly flattened at right angles to the septum, elliptic, oblong, ovate, orbicular, obovate, or obcordate, beakless, sessile [or very rarely borne on a short gynophore], retuse to emarginate [or acute to obtuse] at apex; valves navicular, usually strongly keeled, wingless or extended into a narrow or broad distal wing, 1-nerved, with inconspicuous [or prominent] anastomosing lateral nerves, glabrous or pubescent; replum usually thickened and broader at base; septum narrow, membranaceous, nerveless, elliptic to lanceolate or rhomboid; styles short or long [sometimes obsolete or lacking], included or exerted from the apical sinus of fruit, free or adnate to the apical wing of valve. Seeds 1 per locule, pendulous, narrowly winged or wingless, oblong or oval, rounded or flattened, usually copiously mucilaginous when wet, brown to red or yellow, minutely reticulate; cotyledons entire or very rarely 3-lobed, incumbent or sometimes oblique, very rarely accumbent [or transversely folded (diplecolobous)]. Base chromosome numbers 7, 8, 10, 12. (Including *Cardamon* (DC.) Fourr., *Kandis* Adanson, *Lepia* Desv., *Monoploca* Bunge, *Papuzilla* Ridley, *Sprengeria* Greene.) LECTOTYPE SPECIES: *L. latifolium* L.; see Britton & Brown, *Illus. Fl. No. U. S. & Canada*, ed. 2. 2: 164. 1913. (Name derived from Greek, *lepis*, a scale, or more likely *lepidion*, a little scale, in reference to the appearance of the fruit.)—PEPPERGRASS, PEPPERWORT, CRESS, PEPPERCRESS, TONGUEGRASS.

A cosmopolitan genus of about 175 species distributed primarily in temperate and subtropical regions and poorly represented in the tropics and alpine areas, with some 25 species indigenous in North and Central America, 37 in South America, 47 in Australia, New Guinea, and New Zealand, 22 in Africa, and the remainder in Europe, Asia, and the Hawaiian Islands. The genus is represented in the southeastern United States by 12 species, of which five are indigenous, four are introduced from Europe, and three are “wool-alien” weeds recently reported from waste grounds around wool-combing mills in South Carolina.

Four of the seven well-defined sections recognized by Hewson (1982a) are represented in our area. Section LEPIDIUM (sect. *Lepidiastrum* DC.) (petals present; stamens 6; fruits wingless, without apical sinus; styles exerted) is represented in the Southeast by a single species. *Lepidium perfoliatum* L., shield cress, clasping-leaved peppergrass, $2n = 16$, a native of southwestern Asia and probably eastern and central Europe, is a weed of roadsides, waste places, fields, and pastures in North Carolina, Georgia, Tennessee, Mississippi, Arkansas, and probably the other states of the Southeast and is widely distributed elsewhere in North America. It can easily be distinguished by its bi- or tripinnatisect basal leaves, deeply cordate-amplexicaul cauline leaves, and yellow flowers. Two perennials of sect. LEPIDIUM have been brought into North America, but neither has reached our area. *Lepidium latifolium* L., $2n = 24$, is a

successful weed in parts of North America, while *L. graminifolium* L., $2n = 24$, has failed to persist after its initial appearance as a ballast plant.

The monotypic sect. *CARDAMON* DC. (petals present; stamens 6; fruits narrowly winged, emarginate; styles included in the apical sinus, adnate to the wings; cotyledons 3-lobed) includes only *Lepidium sativum* L., garden cress, cress, $2n = 16, 24$, which is a native of southwestern Asia and northeastern Africa. The species was reported as an escape from cultivation in Tennessee (Gattinger, Hebel), but there is no evidence that it is presently naturalized either in that state or elsewhere in the Southeast.

Of the two species of sect. *LEPIA* (Desv.) DC. (petals present; stamens 6; fruits broadly winged, emarginate; styles exerted from the apical notch, adnate to the wings; cotyledons undivided) naturalized in North America, *Lepidium heterophyllum* (DC.) Benth, $2n = 16$, is sporadic in widely separated areas in British Columbia, California, Colorado, and Massachusetts. The second species, *L. campestre* (L.) R. Br. (*Thlaspi campestre* L.), cow cress, field cress, field peppergrass, poor man's pepper, $2n = 16$, is a native of Europe and Asia Minor that grows in fields, waste places, roadsides, pastures, and gardens throughout our area. It is easily distinguished by its sagittate cauline leaves, exerted styles, and large (5–6 × 3.5–4 mm), broadly winged, inflated fruits covered with small vesicles.

The remaining lepidiums in the Southeast belong to sect. *DILEPTIUM* (Raf.) DC. (petals usually rudimentary or absent; median stamens 2 or 4; fruits narrowly winged or wingless, slightly notched; styles short or obsolete, always included in the sinus), the largest and most diversified section in the genus. *Lepidium virginicum* L., peppergrass, poor man's peppergrass, $2n = 32$, the most widely distributed North American species, probably occurs in every county in the Southeastern States. Of the eight varieties recognized by Hitchcock (1936, 1940, 1945b), *L. virginicum* var. *virginicum* is naturalized on all continents but Antarctica and is the only member of the genus with accumbent cotyledons. Another variety, not previously recorded from the southeastern United States, is *L. virginicum* var. *medium* (Greene) C. L. Hitchc. (*L. medium* Greene, *L. idahoense* Heller, *L. glaucum* Greene), $2n = 32$. It is easily distinguished from var. *virginicum* by its incumbent or oblique cotyledons and its glabrous infructescences. Varietas *medium* is widespread in Texas, Oklahoma, Arizona, and most of the Pacific and Mountain states but is of very restricted distribution and probably introduced in the Southeast (a few collections in Louisiana (*Barkley 37418*, GH; *Lowe 34*, GH), Arkansas (*Demaree 47912*, GH), and Florida (*Brumbach 9171*, GH, and *Wible 801*, A)). The record of *L. Menziesii* DC. from Arkansas (Branner & Coville) probably represents a misidentification of plants of *L. virginicum* var. *virginicum*. Hitchcock (1940) reduced *L. Menziesii* to a variety of *L. virginicum* that is highly localized in Washington.

Another North American species of sect. *DILEPTIUM* is *Lepidium densiflorum* Schrader (*L. neglectum* Thell., *L. apetalum* of North American authors, not Willd.), peppergrass, green-flowered peppergrass, $2n = 32$, which is also naturalized in Europe and parts of Asia. It occurs in all of the Southeastern States but is less abundant than *L. virginicum*. The two species have often been confused, and some authors (e.g., Smith) have reduced *L. densiflorum* to a

synonym of *L. virginicum*, while Radford and colleagues have omitted it (despite its wide distribution). Plants of *L. virginicum* usually have conspicuous petals equal to or longer than the sepals, accumbent cotyledons, orbicular or elliptic fruits widest at the middle, and pubescent (rarely glabrous) inflorescence rachises with curved, usually subappressed, pointed trichomes. The cotyledons in most varieties of *L. virginicum* are oblique, but incumbent ones can be found in vars. *medium* and *Robinsonii* (Thell.) C. L. Hitchc. In addition, plants of this species tend to produce slightly reduced petals toward the end of the season. On the other hand, plants of *L. densiflorum* always have incumbent cotyledons, reduced or rudimentary petals much shorter than the sepals (or absent), obovate or obcordate fruits widest above the middle, and rachises with short, straight, obtuse papillae. Fruit size is unreliable for distinguishing the two species, particularly if the infraspecific taxa of both are considered. The confusion between *L. virginicum* and *L. densiflorum* may be attributed to interspecific hybridization, as has been suggested by several authors, without supportive experimental evidence. Early North American taxonomists confused *L. densiflorum* with the central Asiatic *L. apetalum* Willd., and a few even suggested that our plant is introduced from the Old World. However, *L. apetalum* is very distinct because of its clavate trichomes and elliptic fruits with small, acute wings. *Lepidium densiflorum* exhibits greatest diversity in the United States, where it is represented by several indigenous varieties that support its North American origin.

The third North American native is *Lepidium oblongum* Small (*L. reticulatum* Thell., *L. Greenei* Thell.), $2n = 16$, which is found in Arkansas (Lonoke, Clay, Miller, and Hampstead counties), Louisiana (Bossier Parish; *Thomas 48608* at NLU), Kansas, Oklahoma, Texas, New Mexico, Arizona, California, Mexico, and Guatemala. It is distinguished from the other lepidiums in our area by its pinnatifid to deeply lacinate cauline leaves, prostrate or ascending stems usually branching near the base, and glabrous fruits with acute wings and V-shaped sinus. Hitchcock (1936) suggested that *L. oblongum* is a South American plant but later (1945b) accepted it as North American. The species has recently been reported as a "wool alien" from South Carolina (Al-Shehbaz, 1986).

Lepidium austrinum Small (*L. austrinum* var. *orbiculare* Thell., *L. austrinum* var. *conspicuiiflorum* Thell., *L. lasiocarpum* Nutt. var. *orbiculare* (Thell.) C. L. Hitchc.), $2n = 32$, is another North American member of sect. DILEPTIUM. It is common in Texas, New Mexico, and northern and central Mexico but is rare in Kansas and Oklahoma. Although *L. austrinum* has recently been reported as a "wool alien" from South Carolina, it is probably indigenous to Louisiana. The record (here reported) is based on *Thieret 30012* (GH) from East Carroll Parish, and *Thomas 28857* (NLU) from Grant Parish, Louisiana. The species is distinguished by its hispid stems; dentate or entire cauline leaves; elliptic to ovate siliques with sparse, short, appressed trichomes; and terete or slightly flattened fruiting pedicels with glabrous lower surfaces.

Lepidium lasiocarpum Nutt., which was reported for Louisiana (Thomas & Allen; MacRoberts) and South Carolina (Al-Shehbaz, 1986), is easily confused with *L. austrinum*. Fruits of *L. lasiocarpum* have spreading trichomes, and the fruiting pedicels are either not flattened and with pubescent lower surfaces or

very strongly flattened and with glabrous lower surfaces. I have seen two specimens from Louisiana. One, *Thomas 48606* (NLU), collected from Bossier Parish, belongs to *L. lasiocarpum* var. *Wrightii* (Gray) C. L. Hitchc. The other, *Thomas 34419* (NLU), collected from Ouachita Parish, is intermediate between *L. lasiocarpum* and *L. austrinum*.

The Eurasian *Lepidium ruderae* L. (*L. texanum* Buckley), stinking peppergrass, roadside peppergrass, $2n = 16$, is sporadically distributed in Florida, Alabama, Louisiana, Tennessee, and North Carolina and elsewhere in North America but is more restricted in portions of South America. It is easily distinguished from the other members of sect. DILEPTIUM by its fetid odor, bipinnatifid basal leaves, small ($2-2.5 \times 1.5-2$ mm), ovate to broadly elliptic or oblong fruits with acute apical teeth, and slender pedicels longer than the fruits.

Two other alien representatives of sect. DILEPTIUM have appeared in some of the Pacific States but not elsewhere in the United States. The South American *Lepidium strictum* (S. Watson) Rattan is distributed in California and Oregon, while *L. pinnatifidum* Ledeb., a native of southeastern Russia, is known from a few localities in California. Three other "wool-alien" lepidiums, *L. bonariense* L. (South America), *L. Schinzii* Thell. (Africa), and *L. africanum* (Burman f.) DC. (Africa), have been reported from waste grounds around wool-combing mills in South Carolina (Al-Shehbaz, 1986). They are also "wool-alien" or naturalized weeds in Africa, Australia, and Europe.

Lepidium is a well-defined genus characterized by the angustiseptate, dehiscent, usually notched fruits; the pendulous, usually copiously mucilaginous single seed in each locule; the two or four (sometimes six) stamens; the strongly keeled valves; and the toothlike nectar glands. Its closest relatives are probably *Cardaria* and *Coronopus*, which have indehiscent fruits and usually unkeeled, wingless valves.

Many species of *Lepidium* have been recognized on the basis of minor differences in leaf margin, pubescence, and fruit shape. Species boundaries are sometimes poorly defined, particularly in the polymorphic *L. lasiocarpum*, *L. virginicum*, and *L. densiflorum*, and a few authors have attributed this variation to hybridization. However, natural hybridization has not been documented experimentally, and its occurrence was suggested by Hitchcock (1936, 1945b) and Howell only on the basis of comparative morphology.

Dioecism in the Cruciferae is known only in *Lepidium sisymbrioides*, *L. Kawarau* Petrie, and *L. Matau* Petrie (Allan), all from New Zealand. Thellung (1906b) reduced the last two to subspecies of the first, but whether one or more species are involved, nothing is known about the reproductive biology in this complex.

The flowers of *Lepidium* have several adaptations that enforce or promote autogamy, which is very widespread in the genus. In the majority of species the flowers are reduced in size and scentless. In at least 23 percent of the species (author's compilation) the petals are lacking, and in many others they are either rudimentary or inconspicuous. The reduction in flower size is often accompanied by a decrease in stamen number. Of 156 species surveyed by the author, 83 have flowers with two stamens, 20 have flowers with four, and the remainder have flowers with six. Selfing in many species is brought about by anther

dehiscence in the bud long before anthesis. The flowers in *L. campestre* and *L. sativum* are said to be slightly protogynous (Knuth), and those of the latter may be strongly odoriferous, thus promoting outcrossing to a certain degree.

Chromosome numbers have been reported for about 40 species, of which all except five have $x = 8$ and nearly half are either tetraploid or octoploid. Diploid and tetraploid populations have been found in *Lepidium ruderale* and *L. virginicum*. In *L. sativum* diploid and tetraploid plants based on eight and twelve are known (Goldblatt). Vaarama speculated that *L. sativum* is a hexaploid based on $x = 4$, but this interpretation is not supported by facts.

Benzylglucosinolate or its ring-oxidized (hydroxylated or methoxylated) derivatives characterize nearly all of the dozen or so species analyzed thus far. The annotations of M. G. Ettliger on several sheets in the Gray Herbarium indicate that *Lepidium austrinum* contains benzylglucosinolate, while *L. virginicum* var. *medium* has large amounts of *m*-hydroxybenzylglucosinolate and smaller quantities of the first compound and of methoxybenzylglucosinolate. *Lepidium virginicum* var. *Menziesii* (DC.) C. L. Hitchc. appears to be the single known natural source of ethylglucosinolate (Kjaer & Larsen). The fetid odor produced by *L. ruderale* is caused by benzyl thiocyanate, which results from the hydrolysis of benzylglucosinolate by a special enzyme. The seeds of *L. sativum* contain cucurbitacin, a series of tetracyclic triterpenes very rare in the Cruciferae (Curtis & Meade). Nine species have been surveyed for fatty acids; all show a preponderance of linolenic acid and very little or no erucic acid (Kumar & Tsunoda).

The seed-coat anatomy shows some interspecific differences of taxonomic importance (Jonsell). Cells of the palisade layer have radially and tangentially thickened walls, while those of the epidermis contain large columns of mucilage. Anatomical studies for other parts of the plant are generally lacking. The wood anatomy of the Hawaiian *Lepidium serra* H. Mann and the structure of the fleshy roots of the Peruvian *L. Meyenii* Walp. have been studied by Carlquist and León, respectively.

The seeds of about 85 percent of the species of *Lepidium* (author's compilation) exude an abundant mucilage soon after wetting. Mucilage probably plays an important role in seed germination. It is very strongly developed in species of arid areas (Hewson, 1982a) and in all except three of the weedy species. *Lepidium heterophyllum*, *L. graminifolium*, and *L. bonariense* have very little or possibly no mucilage. Niemi suggested that the mucilage aids in the dispersal of the seeds of *L. ruderale* by gulls.

Lepidium sativum is cultivated as a salad plant for the peppery taste of its seedlings and young shoots. In the highest and coldest cordilleras of central Peru where no other cultivated plants can grow, *L. Meyenii* is cultivated for its fleshy roots that are eaten boiled or roasted and are also used for flavoring rum (León). The seeds of several species are said to be excellent seasoning for salads, soups, and meat dressing (Fernald & Kinsey). Various species were extensively used for treating warts, tumors, asthma, coughs, and liver diseases. Some are said to have aphrodisiac, laxative, rubifacient, antiscorbutic, and diuretic properties (Caius, Hartwell). However, it is doubtful that the medicinal

properties extend beyond being antiscorbutic. *Lepidium* is important for about 20 weedy species of cosmopolitan or localized distribution.

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15. **Coronopus** Zinn, *Cat. Pl. Hort. Acad. Gott.* 325. 1757, nom. cons.

Annual, biennial [or perennial] herbs, glabrous or with simple trichomes [or sometimes with minute tubercles]. Stems usually several to many, prostrate or ascending, very rarely solitary and erect. Basal leaves petiolate, 1- to 3-pinnatisect or pinnatifid, occasionally forming a rosette. Upper cauline leaves short petiolate or sessile, divided [or entire to serrate]. Inflorescence an ebracteate, densely flowered, corymbose raceme, usually axillary or leaf opposed, sometimes terminal or arising directly from the center of rosette, slightly to greatly elongated in fruit; flowers minute, short pedicellate. Sepals spreading, equal, not saccate, caducous or persistent, oblong to elliptic or ovate, usually with a membranaceous margin. Petals undifferentiated [or differentiated] into claw and limb, longer or shorter than the sepals, sometimes reduced to bristles or lacking, white [or violet], oblong or linear-oblong to subulate [or obovate]. Nectar glands [2 or] 4 or 6, minute, usually conical or toothlike. Stamens 6, tetradynamous, sometimes 2 (or 4?) and median; filaments not appendaged, usually dilated at base, caducous [or persistent]; anthers oval, introrse. Fruiting pedicels divaricate [or erect], terete [or flattened]. Fruits indehiscent, strongly flattened at right angles to the septum, broader than long, didymous or reniform to cordate [or obcordate], acute or retuse to emarginate at apex, usually cordate at base; valves 1-seeded, usually nutletlike, with or without an orifice in the area of attachment to the replum, reticulate or coarsely reticulate-rugose to verrucose or tuberculate [or smooth], round or rarely keeled, glabrous [or pubescent]; replum narrowly lanceolate or linear, slender [or thickened], equaling or slightly wider than the fruiting pedicel, persistent [or all or the distal half falling off with the valves]; septum reduced [or lacking]; styles obsolete or prominent, included in the apical notch or exerted and forming the persistent

conical tip of fruit; stigmas capitate. Seeds oblong or reniform [subglobose or oval], sometimes slightly compressed, pendulous, solitary in each locule, non-mucilaginous when wet, minutely reticulate, yellow to light brown; cotyledons incumbent, linear, usually curved near the tip. Base chromosome number 8. (Including *Carara* Medicus, *Cotyliscus* Desv., *Lepicochlea* Rojas Acosta, *Nasturtium* Medicus, *Senebiera* DC.) TYPE SPECIES: *C. Ruellii* All. (*Cochlearia Coronopus* L.) = *Coronopus squamatus* (Forsskål) Ascherson; see Int. Code Bot. Nomencl. 1983, p. 350. (Name used by Dioscorides and Theophrastus, probably for *Plantago Coronopus* L.; derived from Greek, *korone*, crow, and *pous*, foot, in reference to the shape of basal leaves. A few authors mistranslate *korone* to crown and suggest that the name corresponds to the radial spreading of basal leaves and lower branches into a crown.)—WART CRESS, SWINE CRESS.

A well-defined genus of ten species, of which four are indigenous to South America and six to Africa, with the natural range of one extending into southwestern Asia and southern and central Europe. Two species are cosmopolitan weeds, and both occur in the southeastern United States. A third, *Coronopus integrifolius* (DC.) Sprengel, is indigenous to Africa and is now naturalized in Australia and eastern Asia.

Coronopus is divided into four well-marked sections, the limits of which correspond fairly well to those originally defined by De Candolle (1821) and slightly altered by Muschler and Schulz (1933, 1936). The Old World sect. CORONOPUS (sect. *Carara* (Medicus) DC.) (stamens 6; petals present; fruits indehiscent, reniform, not emarginate at apex; styles conical; valves keeled) includes two species, of which one is the perennial *C. violaceus* (Munby) Kuntze. The other, *Coronopus squamatus* (Forsskål) Ascherson (*Lepidium squamatum* Forsskål, *Cochlearia Coronopus* L., *Carara Coronopus* (L.) Medicus, *Senebiera Coronopus* (L.) Poiret, *Coronopus Coronopus* (L.) Karsten, *C. Ruellii* All., *C. procumbens* Gilib., *C. verrucarius* (Gars.) Muschler & Thell.), creeping wart cress, swine cress, crowfoot, $2n = 32$, is a cosmopolitan weed with a native range in southwestern Asia, southern Europe, and northern Africa. It is sporadically distributed in the United States, but although it has been reported from Alabama, Florida, Louisiana, and Tennessee, I have not seen any specimens from the Southeast. *Coronopus squamatus* can be distinguished from the other weedy crucifers in our area by its indehiscent, reniform, acute, coarsely rugose-reticulate fruits; its pinnatisect leaves; and its prostrate, much-branched stems.

Section NASTURTIOLUM (Medicus) DC. (stamens 2; fruits didymous, emarginate at apex, splitting into nutletlike, inflated, unkeeled, 1-seeded halves; styles short or obsolete, included in the apical sinus of the fruit) has four species, of which *Coronopus integrifolius* and *C. zambiensis* Jonsell are native to southern and central Africa and two other species to South America. *Coronopus didymus* (L.) Sm. (*Lepidium didymum* L., *Carara didyma* (L.) Britton, *Senebiera didyma* (L.) Pers., *S. pinnatifida* DC., *S. incisa* Willd., *Cochlearia humifusa* Michx., *Biscutella apetala* Walter), swine cress, wart cress, land cress, $2n = 32$, is a cosmopolitan weed widely distributed throughout the Southeastern States along roadsides and in fields, pastures, lawns, gardens, nurseries, and waste places.

The native range of *Coronopus didymus* is controversial. Some North American authors follow Robinson, who suggested that it was originally introduced into North America from Europe, while a few (e.g., Muenscher) have claimed that it is a Eurasian plant. Other authors consider *C. didymus* a South American plant, a view I agree with for two reasons. First, the nearest relative of *C. didymus* is a South American endemic recently described as *C. leptocarpus* Boelcke. Second, the greatest morphological diversity of *C. didymus* occurs in South America, where several varieties and forms have been recognized (Muschler). It is not known how and when *C. didymus* first appeared in Europe and North America, but it was established in some parts of these continents during the late eighteenth and early nineteenth centuries, as evidenced by its repeated description as new species in both continents.

The North African sect. COTYLISCUS (Desv.) DC. includes *Coronopus niloticus* (Delile) Sprengel, an endemic of Egypt, and *C. lepidioides* (Cosson) Kuntze, which is restricted to parts of Tunisia, Algeria, and Morocco. Section XERORRHIZA O. E. Schulz contains *C. rhytidocarpus* (Hooker) Macloskie, of Patagonia, and *C. serratus* (Poiret) Desv., of Argentina and Uruguay. The latter has been introduced recently in Mauritius (Troncoso & Bacigalupo).

Coronopus is easily distinguished by its axillary or leaf-opposed inflorescences, its coarsely reticulate or verrucose to rugose, usually didymous fruits (FIGURE 1h) that break up at maturity into 1-seeded, nutletlike halves, and its nonmucilaginous seeds. It is closely related to *Lepidium*. Muschler suggested that *Coronopus* may represent the end product of parallel evolutionary trends in *Lepidium* that led to the formation of indehiscent fruits. This implies a polyphyletic origin of *Coronopus*, a view not supported by facts. Although Muschler reduced *Delpinophytum* Spegaz. (= *Delpinoella* Spegaz.) to a subgenus of *Coronopus*, the two are remotely related. The former has tiny imbricate leaves, long styles, linear anthers, and copiously mucilaginous, beaked seeds.

Species of sect. NASTURTIOLUM exhibit reductions in flower size, amounts of nectar secreted, petal size, and stamen number. The two anthers usually dehisce in the bud, and pollination may take place long before anthesis. These features undoubtedly indicate autogamy, but protandry and ant pollination have been reported in *Coronopus didymus* by Chauhan (1979a). Cross pollination and slight protogyny have been observed in *C. squamatus*. Several authors have stated that the flowers of *C. didymus* contain two or four stamens. However, the flowers in all but one of the 198 specimens I examined had only two median stamens. In one plant most flowers had two stamens and only a few had four. The petals in *C. didymus* are reduced into subulate or filiform structures misinterpreted as staminodes (Chauhan, 1982b) or as filaments of sterile median stamens (Smith). According to these authors, the petals are lacking, but this implies that all six stamens have a median position facing the outer sepals, a feature not yet found in any crucifer.

Plants of *Coronopus didymus* produce on average some 1600 seeds, but the output of large plants may be as high as 18,000 seeds (Salisbury). A few authors have suggested that the seeds (actually fruit halves) may be transported by strong winds or by birds (McDowall *et al.*), but Salisbury maintains that the

fruits of *C. didymus* and *C. squamatus* are probably distributed in mud on the hooves of animals and that ants also can carry the fruits.

The seed coats of *Coronopus didymus* and *C. squamatus* have palisade cells with evenly thickened inner tangential walls, but the latter species has two layers of thick-walled subepidermis that are lacking in the former (Vaughan & Whitehouse). This anatomical difference supports the disposition of the two species in separate sections.

The leaves and young plants of *Coronopus squamatus* and *C. didymus* are eaten as a salad in the Caucasus and Argentina, respectively. The latter species is cultivated in northern Argentina and is used as a disinfecting infusion for wounds or is mixed with maté (Paraguay tea), *Ilex paraguariensis* St.-Hil., for certain medicinal purposes (La Porte).

Cattle feeding on *Coronopus didymus* develop a disagreeable flavor in their milk (and consequently in their butter). The off-flavor, caused by benzyl mercaptan and benzyl methyl sulfide (Walker & Gray, Park *et al.*), is intensified by heat treatment and cannot be eliminated by conventional techniques (McDowall *et al.*). These compounds are derived from benzyl thiocyanate, which results from the enzymatic hydrolysis of benzylglucosinolate. It has been estimated that up to 20 percent of the butter produced in Australia is weed tainted.

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16. *Cardaria* Desvaux, Jour. Bot. Appl. 3: 163. 1815.

Perennial herbs, sparsely to densely pubescent with simple trichomes, rarely glabrous. Stems several, erect or rarely decumbent, arising from subterranean rhizomes. Basal leaves petiolate, usually sinuate or lyrate, sometimes dentate or entire. Cauline leaves sessile, sagittate or cordate to auriculate or amplexicaul at base, dentate to denticulate or rarely entire. Inflorescence an ebracteate, densely flowered, corymbose panicle, often slightly elongated in fruit. Sepals erect or spreading, oblong to ovate, not saccate, glabrous [or pubescent], caducous, membranaceous at margin. Petals white, clawed, obovate to spatulate; claw about as long as the limb, usually dilated at base. Nectar glands continuous, subtending the bases of stamens. Stamens 6, tetradynamous; filaments free, not appendaged; anthers oblong or ovate, introrse. Ovary sessile, 2- or 4-ovulate, glabrous [or pubescent]; style usually almost as long as the ovary; stigma capitate, entire, broader than the style. Fruiting pedicels slender, usually spreading. Fruits indehiscent, ovoid or cordate to reniform [or obovoid or subglobose], compressed at right angles to the septum [or not compressed], slightly [to strongly] inflated, glabrous [or pubescent]; valves prominently [or obscurely] 1-nerved, somewhat keeled [or round], reticulate [or smooth]; septum elliptic [or suborbicular], complete [or fenestrate]. Seeds usually 1 per locule, ovoid or ellipsoid, pendulous, wingless, minutely reticulate, reddish brown, mucilaginous when wet; cotyledons incumbent. Base chromosome number 8. (Including *Cardiolepis* Wallr., *Hymenophysa* C. A. Meyer, *Physolepidion* Schrenk.) TYPE SPECIES: *Lepidium Draba* L. = *C. Draba* (L.) Desv. (Name from Greek, *kardia*, heart, in reference to the cordate fruits of some members of the genus.) —HOARY CRESS, WHITE TOP.

A genus of two species native to the Mediterranean and Irano-Turanian regions and widely distributed as naturalized weeds elsewhere in the world, especially in temperate regions, where they grow in fields, waste places, pastures, disturbed sites, and gardens, as well as along roadsides, railroad tracks, and irrigation ditches. *Cardaria* is widespread in the western United States and western Canada but is sporadic in eastern North America and Mexico. It was first collected in the United States in 1862 and in Canada in 1878 (Mulligan & Frankton).

Although *Cardaria Draba* (L.) Desv. (*Lepidium Draba* L., *Cochlearia Draba* (L.) L.), heart-podded hoary cress, hoary pepperwort, white top, is said to be distributed in all of the Southeastern States except Louisiana (Reed), I have not seen any specimens from the Southeast, and the species has not yet been collected from this area. The genus, however, is included here because it occurs in all of the neighboring states and is likely to be found in northeastern Arkansas (Smith).

Some of the many morphological extremes of *Cardaria Draba* have been recognized as distinct species (Rollins, 1940; Mulligan & Frankton). At least two of these are well defined and deserve specific rank. Two subspecies can be recognized in *C. Draba*, but because they are aggressive, perennial, rapidly spreading weeds of similar habitats, they do not have sharply defined ranges. In general, subsp. *Draba* tends to be Mediterranean, while subsp. *chalepensis*

(L.) O. E. Schulz (*Lepidium chalepense* L., *Physolepidion repens* Schrenk, *C. chalepensis* (L.) Hand.-Mazz., *C. repens* (Schrenk) Jarmolenko, *Hymenophysa macrocarpa* Franchet, *C. macrocarpa* (Franchet) Rollins, *H. fenestrata* Boiss., *C. fenestrata* (Boiss.) Rollins, *L. propinquum* (Fischer & Meyer) N. Busch), lens-podded hoary cress, probably is an Irano-Turanian element (Hedge). Both taxa are treated as species by some North American authors and as subspecies by authors elsewhere. I and many others prefer to recognize them as subspecies because they are interfertile and can only be separated by a few continuous characters of the mature fruits. In subsp. *Draba* the fruits are clearly compressed, somewhat carinate, slightly inflated, and usually cordate at the base, while in subsp. *chalepensis* they are slightly compressed, only weakly or not carinate, more inflated, and usually truncate or obtuse at the base. The perforation of the septum shows continuous variation not associated with other morphological characters. Therefore, *C. fenestrata*, which has an incomplete septum, cannot be maintained as a distinct taxon.

Cardaria pubescens (C. A. Meyer) Jarmolenko (*Hymenophysa pubescens* C. A. Meyer), a native of central Asia, is a common, aggressive, and noxious weed in western Canada and the western United States but is only occasional in some other parts of North America. It is easily distinguished from other members of the genus by its sparsely to densely pubescent, noncarinate, strongly inflated fruits.

Although earlier authors (e.g., De Candolle (1821, 1824), Bentham & Hooker, Thellung) reduced *Cardaria* to a section of *Lepidium*, there are significant differences that support maintaining both genera. The fruits of *Cardaria* are indehiscent, inflated, wingless, only slightly or not carinate, and entire at the apex, while those of *Lepidium* are dehiscent, not inflated, strongly compressed contrary to the septum, always keeled, often winged, and emarginate at the apex. Furthermore, the nectar glands in *Cardaria* are continuous and subtend the bases of all stamens; those of *Lepidium* usually form four or six separate teeth. *Hymenophysa* is not sufficiently distinct from *Cardaria* and differs only by its subglobose fruits with a broad septum. Schulz recognized both genera but placed *Cardaria* in the Lepidieae and *Hymenophysa* in the Euclidieae.

The flowers of *Cardaria Draba* are inconspicuous, sweetly scented, and grouped in dense corymbose panicles that are visited by several kinds of insects, particularly bees of the genus *Halictus* (Halictidae) and beetles of the genera *Meligethes* (Nitidulidae) and *Nacerdes* (Oedemeridae) (Knuth). The flowers are protogynous or not and do not reflect ultraviolet light. Both species of *Cardaria* are self-incompatible (Mulligan & Findlay).

Chromosome numbers based on eight characterize both species of *Cardaria*, but the genus is cytologically more complicated than shown by Mulligan & Frankton. The limited number of chromosome counts indicates that *C. pubescens* is diploid ($2n = 16$), while *C. Draba* subsp. *Draba* is tetraploid ($2n = 32$) or octoploid ($2n = 64$) and subsp. *chalepensis* is hexaploid, octoploid, or decaploid (Al-Shehbaz & Al-Omar, Aryavand, Podlech & Dieterle). Natural hybrids between octoploid plants of subsp. *Draba* and decaploid ones of subsp. *chalepensis* are fully fertile enneaploids ($2n = 72$), but the chromosome num-

bers of their offspring range from 66 to 72 (Mulligan & Frankton). Obviously, the genus needs further studies of cytology and hybridization.

Seeds of *Cardaria Draba* subsp. *Draba* contain large amounts of 4-methylthiobutyl and 4-methylsulfinylbutyl glucosinolates (Daxenbichler *et al.*, Procházka), as well as *p*-hydroxybenzylglucosinolate (Al-Shehbaz, unpublished). The green parts contain other glucosinolates not encountered in the seeds (Hasapis *et al.*, Dornberger *et al.*). The other taxa of the genus have not yet been subjected to chemical analyses.

Some anatomical peculiarities of *Cardaria* include the presence of root-hair-like trichomes on the stem just below ground level, the occurrence of large intercellular spaces in the rhizome, and the resemblance of its compact leaf structure (with extremely small, very numerous stomata estimated at 173,355 per square inch) to that of xerophytic plants (Simonds). In seed-coat anatomy *Cardaria* differs from other members of the Lepidieae in having an epidermis with strongly thickened inner tangential walls, a palisade layer with highly thickened radial and inner tangential walls, and a pigment layer three cells thick (Vaughan & Whitehouse).

Cardaria Draba is very difficult to eradicate and is a serious competitor that reduces the yield of wheat lands. Cattle feeding on the plant produce tainted milk and butter. The plant is eaten as a salad or cooked as a potherb in some parts of the Mediterranean region and central Asia. It is also used as fodder. The seeds have a peppery taste and were formerly used as a substitute for pepper.

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17. **Thlaspi** Linnaeus, *Sp. Pl.* 2: 645. 1753; *Gen. Pl.* ed. 5. 292. 1754.

Annual [or biennial or perennial] herbs, glabrous or very rarely with simple trichomes, often glaucous. Stems one or usually several from the base. Basal leaves petiolate [or sessile], forming a distinct rosette or not, entire or dentate to sinuate [rarely pinnately lobed]. Cauline leaves glabrous, sessile, usually amplexicaul, sagittate or auriculate [or very rarely exauriculate] at base, entire or rarely toothed. Inflorescence an ebracteate, densely flowered, corymbose raceme, greatly [or scarcely] elongated in fruit; infructescence loose [or compact]; fruiting pedicels glabrous, usually divaricate. Sepals oblong to ovate, erect, glabrous, equal, not saccate, membranaceous at margin, green [pink or purple]. Petals oblong or oblanceolate to obovate, obtuse [or emarginate], white [rose, purple, or rarely yellow], short [or long] clawed, equaling to twice as long as the sepals. Nectar glands usually present on each side of the lateral stamens, median glands lacking. Stamens 6, tetradynamous; filaments linear, free, not appendaged; anthers ovoid [or oblong]. Ovary sessile, glabrous. Fruits dehiscent, glabrous, strongly [rarely weakly] flattened at right angles to the septum, obcordate to suborbicular [oblanceolate, obovate, obtriangular, or lanceolate], emarginate [or retuse, truncate, obtuse, or acute] at apex, obtuse to cuneate [or attenuate] at base; valves navicular, keeled, nerveless or obscurely nerved, uniformly broad winged [or winged above the middle, or wingless, or terminating in a horn]; replum ovate to lanceolate, usually asymmetric; styles persistent, short to obsolete [or very long and nearly equaling the rest of the fruit], included in the apical sinus [or exerted]; stigmas capitate, entire [or slightly 2-lobed]. Seeds [1 or] 2–6(–10) per locule, ellipsoid or ovoid, often somewhat compressed, wingless, smooth or with concentric, rugose ribs [or papillose or alveolate to slightly reticulate], yellow to dark brown or black, mucilaginous or not when wet; cotyledons accumbent [or very rarely incumbent]. Base chromosome number 7. (Including *Apterygia* (Ledeb.) Galučko (non Baehni), *Atropatenia* F. K. Meyer, *Callothlaspi* F. K. Meyer, *Carpoceras* Link, *Cruciundula* Raf., *Kotschyella* F. K. Meyer, *Masmenia* F. K. Meyer, *Microthlaspi* F. K.

Meyer, *Neurotropis* (DC.) F. K. Meyer, *Noccaea* Moench, *Noccidium* F. K. Meyer, *Pterotropis* (DC.) Fourr., *Raparia* F. K. Meyer, *Syrenopsis* Jaub. & Spach (non *Syreniopsis* Fuchs), *Thlaspiceras* F. K. Meyer, *Vania* F. K. Meyer.) LECTOTYPE SPECIES: *T. arvense* L.; see Britton & Brown, *Illus. Fl. No. U. S. & Canada*, ed. 2. 2: 167. 1913. (Name mentioned by Hippocrates for a plant, the crushed seeds of which were used as mustard; derived from Greek, *thlaō* (or *thlaein*), to crush, and *aspis*, shield, in reference to the fruits, which are flattened as if crushed.)—PENNY CRESS.

A taxonomically difficult genus of about 75 species, distributed primarily in the subarctic and the North Temperate Zone of Eurasia, particularly in southern and central Europe, Turkey, and the Caucasus, with five species in western North America, one (*Thlaspi magellanicum* Pers.) in subantarctic South America, and none in either Africa or Australia. Except for the highly polymorphic and widespread *T. montanum* L. of Eurasia and the United States (all of the Pacific, Mountain, and Southwestern states, except Oklahoma), the remaining indigenous North American species, *T. mexicanum* Standley (in the high mountains of Nuevo León, Mexico), *T. arcticum* A. E. Pors. (along the Arctic coast of Alaska and the Yukon Territory), *T. Aileeniae* Rollins (Custer County, Idaho), and *T. parviflorum* A. Nelson (central Idaho to western Wyoming and Montana), are somewhat narrowly distributed or highly localized endemics. The genus is represented in the southeastern United States by three weedy European species.

The genus has been divided into five or six sections on the basis of fruit shape, seed-coat configuration, and elaboration of the wing of the fruit. Several recent authors (e.g., Clapham, Hedge (1965b), and Markgraf) have followed De Candolle (1821), Schulz, and Busch in assigning the lectotype species of *Thlaspi* to sect. *Nomisma* DC. instead of sect. THLASPI, therefore contradicting Article 22 of the ICBN. Section THLASPI (sect. *Nomisma*) (fruits suborbicular, uniformly broad winged, emarginate; styles very short, included in the apical sinus of the fruit; seeds concentrically ribbed) contains three species, of which one is a cosmopolitan weed that occurs in all of the Southeastern States. *Thlaspi arvense*, penny cress, field penny cress, stinkweed, frenchweed, fanweed, $2n = 14$, grows in our area along roadsides and in fields, cultivated land, waste places, and gardens. It is easily distinguished from other crucifers of the Southeast by the sectional characters outlined above.

Thlaspi sect. PTEROTROPIS DC. (sect. *Neurotropis* DC., sect. *Euthlaspi* Prantl, sect. *Chaunothlaspi* O. E. Schulz) (fruits narrowly to broadly obcordate, uniformly winged all around or winged only above the middle; styles long, exerted or sometimes included in the apical notch of the fruit; seeds smooth to alveolate) is somewhat heterogeneous and encompasses the bulk of the genus, including all of the New World taxa. *Thlaspi perfoliatum* L. (*Microthlaspi perfoliatum* (L.) F. K. Meyer), penny cress, $2n = 14, 28, 42, 70$, is a Eurasian plant sporadically distributed along roadsides and in fields, waste places, flood plains, and limestone cliffs in North Carolina, Tennessee, and Arkansas. It differs from *T. arvense* in its smooth and fewer (2 to 4 per locule) seeds, cordate cauline leaves, and smaller (5–7 mm long) fruits.

Another species of sect. PTEROTROPIS is *Thlaspi alliaceum* L., $2n = 14$, which was reported by Radford and colleagues from Rockingham County, North Carolina. This record, which is based on a single collection (*Ahles & Radford 10757* at NCU!), appears to be the first for North America. The species has recently been collected in Indiana and Kentucky (Rollins, pers. comm.). *Thlaspi alliaceum* is easily distinguished by its annual habit; pubescent lower stems; subappressed, oblong, dentate, sagittate cauline leaves; very narrowly winged, slightly inflated, obovate or obcordate fruits; and four or five alveolate seeds in each locule.

The other sections of *Thlaspi*, APTERYGIUM Ledeb. (ca. ten species), CARPOCERAS DC. (ca. nine spp.), and SYRENOPSIS (Jaub. & Spach) Hedge (two spp.), are exclusively Eurasian and contain no weedy taxa.

Thlaspi is a relatively well-marked genus most closely related to and sometimes confused with *Aethionema*. The latter is distributed from the Mediterranean region eastward into Afghanistan and adjacent central Asia, but its center of greatest diversity is in central and eastern Turkey. In general, *Thlaspi* is distinguished by its linear, unappendaged, free filaments and its two- to six- (rarely one- or to ten-)seeded locules. The filaments in *Aethionema* are dilated, winged, or toothed, and those of the median pair of stamens often fuse. The locule usually contains one or very rarely to four seeds. The annual species of *Aethionema* often produce heterocarpic fruits borne usually in compact infructescences, while the perennials often have broadly winged fruits and usually have pink flowers. These combinations of characters are not found in any of the approximately 30 annual and 45 perennial species of *Thlaspi*.

Meyer (1973) segregated *Thlaspi* into 12 poorly defined segregate genera, the boundaries of which were drawn primarily on the basis of minor anatomical differences in the seed coat (see also Meyer, 1979). Of the 107 species recognized by Meyer from Europe, Africa, and the Middle East, only six (in three sections and two series) were retained in *Thlaspi* sensu stricto. In my opinion *Thlaspi* (as traditionally delimited) is a natural group, and I cannot find adequate grounds for dividing it into smaller segregates.

Self-compatibility and autogamy are common in *Thlaspi*. In *T. arvense* and *T. alpestre* L. the stigmas and anthers are held at the same level, and self-pollination results from contact between the stigma and the introrse anthers brought about by the inward bending of the staminal filaments. In the European *T. rotundifolium* (L.) Gaudin and *T. alpinum* Crantz the anthers, which are held below the level of the stigma, turn outward, and autogamy is therefore reduced or prevented. Several species with long styles are protogynous. Riley observed that the stigmas of *T. alpestre* protrude from the floral bud three days before anthesis. During this period the stigmas are receptive, and protogyny and insect visitation account for about five percent cross-pollination in the species.

The flowers of *Thlaspi arvense* are occasionally visited by species of the bee genera *Apis* (Apidae), *Halictus*, and *Dialictus* (Halictidae), the fly genera *Anthomyia* (Anthomyiidae), *Pollenia* (Muscidae), *Eristalis*, *Metasyrphus*, and *Helophilus* (Syrphidae), and the butterfly *Pieris rapae* (Pieridae). Holmgren and Rochow observed many species of these insect families and of Chrysomelidae

(leaf beetles), Bombyliidae (bee flies), Andrenidae (mining bees), and Miridae (bugs) visiting *T. montanum* in Washington and Wyoming. Peterson (1977a, 1977b) demonstrated that *T. montanum* is pollinated in the alpine tundra of Colorado by the beetle *Phyllotreta albionica* (Chrysomelidae) and by the ant *Formica neorufibarbis gelida* (Formicidae). The reproductive biology of the majority of species has not been studied. Protogyny and autogamy may be more widespread in the genus than is known.

Chromosome numbers have been reported for about 45 species, of which all except *Thlaspi rivale* J. & K. Presl ($2n = 26$; Franzén & Gustavsson) are uniformly based on $x = 7$. The majority of species are diploid. However, *T. alpinum*, *T. montanum*, and *T. perfoliatum* have both diploid and polyploid populations, while the European *T. goesingense* Halácsy and the Asiatic *T. cochleariforme* DC. are exclusively polyploid. The last species consists of octoploid ($2n = 56$) and 12-ploid ($2n = 84$) populations (Zhukova & Petrovsky, Zhukova *et al.*). All of the New World taxa are diploid, but *T. montanum* var. *montanum* and var. *idahoense* (Payson) P. Holmgren also have tetraploid populations. No counts have been made of *T. mexicanum*. Most counts for *T. perfoliatum* indicate a hexaploid level ($2n = 42$), and although diploid, tetraploid, and decaploid populations have been found (Favarger *et al.*, Hill, Jaretsky), the cytogeography of the species is still poorly understood.

The extensive intraspecific crosses conducted by Holmgren indicate that cross-fertility ranges between 31 and 85 percent in *Thlaspi alpestre* and between zero and 100 percent in *T. montanum*. Crossability between *T. magellanicum* and *T. parviflorum* was 25 to 100 percent and was somewhat lower between the former and *T. montanum* when *T. montanum* was used as the maternal plant. Although the crossability between these species was sometimes high, the first- and second-generation hybrids were largely sterile. The cross *T. alpestre* \times *T. montanum*, however, produced fertile first-generation hybrids.

Natural interspecific hybridization appears to be uncommon in *Thlaspi*. Markgraf listed the hybrid between *T. alpinum* var. *sylvium* (Gaudin) Rouy & Foucaud and *T. rotundifolium* var. *corymbosum* (Gay) Gaudin (as *T. \times Gremlianum* Thell.), but there is no supporting experimental evidence. Many infraspecific taxa, some of which probably merit specific rank, have been recognized in *T. alpestre*, *T. alpinum*, *T. praecox* Wulfen, and *T. rotundifolium*. The taxonomy of these species complexes is rather difficult, and hybridization may have played an important role in their evolution. The affinity of the Asiatic *T. cochleariforme* and the North American and European *T. montanum* is not clear, and although Holmgren reduced the former to a synonym of the latter, *T. cochleariforme* differs in its higher ploidy levels and its unequal petals.

The chemistry of *Thlaspi* has not been studied adequately, and only a few species have been surveyed for fatty-acid composition and for mustard-oil glucosides. Rodman & Chew found large amounts of allylglucosinolate and smaller ones of benzyl and 3-methylsulfinylpropyl glucosinolates in the leaves of *T. arvense*. In the leaves of *T. montanum* they detected traces of isopropyl and 2-butyl glucosinolates in addition to a major constituent tentatively identified as *p*-rhamnopyranosyloxybenzylglucosinolate. Gmelin & Virtanen dis-

covered in *T. arvense* an enzyme that converts allylglucosinolate into allyl thiocyanate, which is responsible for the unpleasant garlicky odor, but Rodman & Chew did not detect this thiocyanate in their sample.

Seeds of *Thlaspi alpestre*, *T. arvense*, and *T. perfoliatum* have been analyzed for fatty acids (Miller *et al.*). Although they differ from the other members of the Lepidieae in the higher concentrations of erucic acid and lower amounts of linolenic and eicosenoic acids combined (Kumar & Tsunoda), neither *Thlaspi* nor the rest of the tribe has been satisfactorily sampled, and any generalizations are, at best, tenuous.

Two informal groups can be recognized in *Thlaspi* on the basis of the thickening of the radial cell walls of the seed-coat palisade. Meyer (1973, 1979) retained six species with such thickened cell walls in *Thlaspi* sensu stricto despite their marked differences in fruit morphology and seed-surface configurations. He divided the rest of the genus into 11 segregates (all with a thin-walled palisade layer) that differ in fruit morphology and in certain features of the outer epidermis of the seed coat (e.g., cell size and presence or absence of mucilage and the central column). It seems that seed-coat anatomy offers no more than a minimal support to the sectional classification of *Thlaspi*.

Although Howitt (cited in Best & McIntyre, 1975) indicated that the seeds of *Thlaspi arvense* are chiefly dispersed by wind, it is more likely that they are transported with those of various crops. Viable seeds have been found in the dung of cattle and horses and in the droppings of birds. They may retain 11 percent viability after burial for 30 years (Salisbury). The seeds of *T. parviflorum* may be the lightest in the genus (averaging 0.17 mg) and can be easily distributed by wind or rain wash, while those of *T. arvense* are the heaviest, ranging from 0.81 to 1.78 mg (author's compilation). The seeds of *T. perfoliatum* are mucilaginous when wet and may be transported by adhesion to animals.

Early- and late-flowering strains have been discovered in *Thlaspi arvense*. The seasonality of flowering is controlled by simple Mendelian inheritance, and late flowering is dominant. The expression of this character, however, may be altered by vernalization, photoperiod, temperature, and nitrogen supply (McIntyre & Best, 1978).

Several infraspecific taxa of *Thlaspi alpestre*, *T. montanum*, and *T. rotundifolium* grow on soils with moderate to high nickel and zinc content. Reeves & Brooks have indicated that at least 12 species of *Thlaspi* show unusual accumulation of nickel (to 1000–30,000 $\mu\text{g/g}$ of dry mass) and that 30 European species accumulate zinc to levels higher than 1000 $\mu\text{g/g}$ of the dry mass. The scant data indicate that zinc probably promotes seed germination. Reeves, MacFarlane, & Brooks have suggested that the hyperaccumulators of nickel in *T. montanum* (three varieties) evolved from var. *montanum* growing on non-mineralized soils.

Females of the butterfly *Pieris napi* deposit eggs on the toxic *Thlaspi arvense* without discriminating between it and some of the native western North American crucifers. The larvae apparently die even from the slightest nibble of this plant (Krivda). Rodman & Chew suggested that the repellency and toxicity of *T. arvense* may be attributed to 3-methylsulfinylpropylglucosinolate (or more

likely its isothiocyanate derivative), but Feeny indicated that larval mortality is caused by benzyl thiocyanate, which was not detected in the samples of Rodman & Chew.

Cattle eating considerable quantities of *Thlaspi arvense* may develop hemorrhagic diarrhea, chronic enteritis, gastric distress, nephritis, colic, abortion, apathy, and paralysis of the heart and lungs (Best & McIntyre, 1975). Milk obtained from cows feeding on this plant often develops an unpleasant flavor. Marked reduction in the yield of wheat has been observed in fields heavily infested by the plants. The seeds of *T. arvense* are employed in China to treat eye diseases and as a tonic (Perry), and in Spain as a stimulant and astringent (Caius). The large ornamental fruits of *T. arvense* are often used in dried plant arrangements, the young leaves are said to be edible, and the seeds are occasionally used as a condiment. *Thlaspi rotundifolium* is cultivated as an ornamental rock-garden plant; it forms compact tufts and produces fragrant rose-lilac flowers.

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18. **Teesdalia** R. Brown in Aiton f. *Hortus Kew.* ed. 2. **4**: 83. 1812.⁵

Annual, usually scapose herbs, glabrous or with simple trichomes. Stems erect or ascending, usually several from the base. Basal leaves petiolate, always in a well-developed rosette, oblanceolate to spatulate [or lanceolate], lyrate to pinnatifid or rarely entire; lateral lobes obtuse [or acute], usually smaller than the terminal one. Cauline leaves (when present) several, small, sessile, linear

⁵Both *Teesdalia* and *Guepinia* Bast. are based on *Iberis nudicaulis* L. According to Stafleu & Cowan (*Regnum Veg.* **94**: 26, 137. 1976), *Guepinia* and *Teesdalia* were published in July, 1812, and December, 1812, respectively. It is clear, therefore, that *Teesdalia* was illegitimate when published. As clearly indicated by Greuter, *Guepinia* Bast., which is an earlier homonym of *Guepinia* Fries and of two other names of fungi (Martin), cannot be adopted because Article 13.1d of the International Code of Botanical Nomenclature (1983, p. 12) states that the names of fungi adopted by Fries “are sanctioned, i.e., are treated as if conserved against earlier homonyms and competing synonyms.” Therefore, *Guepinia* Bast. should be considered rejected.

or oblong, entire or toothed, widely spaced. Inflorescence an ebracteate corymbose raceme, greatly elongated in fruit. Sepals ovate, equal, not saccate at base, ascending to spreading, membranaceous at margin, glabrous. Petals white, obovate to oblong, not clawed; the outer pair much larger than [or subequaling] the inner pair. Nectar glands 4, minute, 1 on each side of the lateral stamens. Stamens 6 and tetradynamous [or 4, equal, and median]; filaments free, linear, white, each with a broadly oblong to ovate or obovate, scalelike, basal appendage appressed to the ovary; anthers oval. Ovary sessile, glabrous, 4-ovulate. Fruiting pedicels slender, divaricate, glabrous or pubescent. Fruits dehiscent, broadly cordate, strongly compressed at right angles to the septum, concave above, convex below, emarginate, glabrous; valves navicular, strongly keeled, margined or narrowly winged distally, with weakly anastomosing nerves; replum \pm straight or slightly concave adaxially, strongly convex abaxially; style very short [or absent], included in the apical notch of the fruit; stigma capitate. Seeds 2 per locule, 1 apical and 1 lateral, brown, obovate, slightly flattened, minutely reticulate, wingless, copiously mucilaginous when wet; cotyledons accumbent. Base chromosome number 9. (Including *Folis Dulac*; *Guepinia* Bast., non Fries nec Hepp.) TYPE SPECIES: *Iberis nudicaulis* L. = *Teesdalia nudicaulis* (L.) R. Br. (Name commemorating Robert Teesdale, ?–Dec. 25, 1804, English botanist and horticulturist.)—SHEPHERD'S CRESS.

A very well-defined genus of two species native to Europe, Cyprus, Turkey, adjacent Russia, and northwestern Africa. Members of the genus grow primarily on sandy soil along roadsides and in fields, lawns, and waste areas. Both species are established in parts of North America, and one occurs in the southeastern United States.

Teesdalia nudicaulis (L.) R. Br. (*Iberis nudicaulis* L., *T. Iberis* DC.), shepherd's cress, $2n = 36$, a native of northern and central Europe and an alien in Australia and northwestern Africa, is a naturalized weed infrequently distributed in states of the eastern seaboard (Massachusetts southward into North Carolina) and in Oregon, Washington, and British Columbia. The second species, *T. coronopifolia* (J. P. Bergeret) Thell. (*Thlaspi coronopifolium* J. P. Bergeret, *Lepidium nudicaule* L., *Teesdalia Lepidium* DC.), $2n = 36$, recently reported from California (Quibell & Strother), is a native of southern Europe, Cyprus, Turkey, and northwestern Africa. The two species are superficially similar, but *T. nudicaulis* has obtusely lobed basal leaves, unequal petals, six stamens, and short styles, while *T. coronopifolia* has acutely lobed basal leaves, subequal petals, four stamens, and no styles.

The genus is closely related to *Thlaspi*, and Von Hayek derived it directly from this, while Schulz placed it between *Ionopsidium* (DC.) Reichenb. and *Pachyphragma* (DC.) Reichenb. in subtribe Thlaspidinae Hayek. *Teesdalia* is easily distinguished from these by its pinnatifid rosette leaves, its leafless or very-few-leaved stems, and its appendaged filaments. Species of *Teesdalia* are tetraploids based on nine. Those of *Thlaspi* are diploids and polyploids uniformly based on seven, while species of *Ionopsidium* are diploids with $n = 11$ or 12 or tetraploids based on eight.

Both species of *Teesdalia* are self-compatible. According to Knuth, the flow-

ers of *T. nudicaulis* are visited by many species of insects, including beetles, flies, and bees, particularly members of the genus *Halictus* (Halictidae-Hymenoptera). The species has some peculiar floral features, such as the unequal petals (which give the inflorescence the appearance of a radiate corymb) and the petaloid basal appendages of the staminal filaments (which aid in the accumulation of nectar drops).

The seed oil of *Teesdalia nudicaulis* contains 56 percent eicosenoic acid. The species is among the crucifers richest in this fatty acid and is second only to *Selenia grandis* R. F. Martin, which has a slightly greater percentage (Appelqvist, Kumar & Tsunoda). The seedlings of *T. nudicaulis* contain 2-phenylethylglucosinolate (Cole), but the seeds of this species and of *T. coronopifolia* have not been analyzed.

The seed coat of *Teesdalia* is composed of a mucilaginous epidermis (with a large hollow column on the inner wall of each cell) above thin-walled palisade and pigment layers and a thick-walled aleurone layer (Vaughan & Whitehouse). Seeds of *T. nudicaulis* have an average weight of 0.20–0.23 mg and exude abundant mucilage when moistened. They are probably dispersed by adhesion to animals.

Except for the weedy tendencies of *Teesdalia nudicaulis*, the genus has no economic importance.

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19. **Capsella** Medicus, *Pflanzen-Gatt.* 85, 99. 1792, nom. cons.

Annual or biennial herbs with simple, furcate, and stellate trichomes. Stems one to several from the base, glabrous or pubescent above. Basal leaves petiolate, usually forming a distinct rosette, very variable in shape and margin, usually entire to lyrate or pinnately lobed. Cauline leaves sessile, usually amplexicaul, auriculate, or sagittate at base, entire to dentate or sinuate. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; fruiting pedicels slender, ascending to spreading. Sepals erect to ascending, oblong to ovate, glabrous or pubescent, not saccate at base, green and with white to red, usually membranaceous, broad margins. Petals obovate to spatulate, white, pink, or red, very rarely yellowish, clawed, as long as or much longer than the sepals, rarely absent. Nectar glands 4, pyramidal or semicircular, 1 on each side of the lateral stamens. Stamens 6, tetradynamous; filaments free, linear, not appendaged; anthers introrse, ovoid to oblong. Ovary sessile, many ovulate, glabrous or very rarely pubescent. Fruit dehiscent, strongly flattened at right angles to the septum, narrowly to broadly obtriangular-cordate, wingless, cuneate at base, emarginate to truncate at apex; valves glabrous, navicular, thin, keeled, obtuse to acute at apex, prominently veined, with the lateral nerves anastomosing near the midvein and usually parallel near the replum; replum narrowly elliptic to lanceolate; septum complete; style short, included or slightly exerted from the apical sinus of fruit; stigma capitate. Seeds (6–)10–20 per locule, brown, oblong, reticulate, mucilaginous when wet, wingless; cotyledons incumbent. Base chromosome number 8. (Including *Bursa* Boehmer, *Rodschiedia* Gaertner, Meyer, & Scherb., *Solmsiella* Borbás.) TYPE SPECIES: *Thlaspi Bursa-pastoris* L. = *C. Bursa-pastoris* (L.) Medicus, typ. cons.; see *Int. Code Bot. Nomencl.* 1983, p. 351. (Name a diminutive of Latin *capsa*, a box or a case, in reference to the form of fruit, which resembles the medieval wallet or purse.)—SHEPHERD'S PURSE.

A monotypic genus with several infraspecific taxa native to Europe and naturalized elsewhere as cosmopolitan weeds. *Capsella Bursa-pastoris* (L.) Medicus (*Thlaspi Bursa-pastoris* L., *Bursa Bursa-pastoris* (L.) Britton; see Index Kewensis for more than 250 additional synonyms under *Capsella* and *Bursa*), shepherd's purse, pickpocket, shovel weed, hen pepper (Small), $2n = 16, 32$, was introduced into North America from Europe long before the eighteenth century and is generally considered to be the most widely distributed crucifer and the second most widely distributed weed on earth (Coquillat). It grows along roadsides and in waste places, lawns, gardens, and cultivated grounds throughout the Southeastern States.

There has been some controversy in treatment of *Capsella* as monotypic or, alternatively, as consisting of four or more species. Undoubtedly, the 200 or more "species" recognized by Almquist (1907, 1921, 1923, 1929) and Shull (1929), which are based on very minor differences in the shape of the basal leaves and fruits, are nothing but biotypes of *C. Bursa-pastoris*. The variation in nearly all features is continuous, and it is often difficult to draw meaningful and reliable lines in this complex. The genetic bases for most of the variation in leaf and fruit morphology were shown by Shull to be controlled by simple Mendelian inheritance, the phenotypic expression of which can be altered by the environment.

Chater recognized five species in *Capsella* separated primarily by petal color and by petal and style lengths. However, Svensson has clearly demonstrated that these characters are unreliable and that the difference in chromosome number between *C. Bursa-pastoris* and *C. rubella* Reuter does not correlate with curvature of the lateral margins of fruit, petal/sepal ratio, color of sepals and petals, or habitat and geographic distribution. These alleged differences in morphology do not correlate with each other either, but they have been utilized in many floras (e.g., Chater, Fernald, Hedge, Markgraf) as the bases for separating *C. Bursa-pastoris* from *C. rubella*. In my opinion, Svensson is fully justified in treating *Capsella* as monotypic, in considering *C. rubella* as a variant not deserving specific rank, and in suggesting that *C. grandiflora* (Fauché & Chaub.) Boiss. and *C. thracica* Velen. may merit no higher than subspecific rank. A similar conclusion was reached earlier by Davis & Heywood, who suggested (p. 379) that "... the taxonomy of the group remains intractable beyond the recognition of the one species, *C. Bursa-pastoris*, containing a number of infraspecific taxa." *Capsella rubella* and *C. grandiflora*, which represent the two opposite extremes in floral morphology in the genus, produce fully fertile hybrids (Riley, 1932) and are indistinguishable in their fatty-acid composition (Mukherjee *et al.*) and in seed-coat anatomy (Vaughan & Whitehouse). Plants comparable to *C. rubella*, as interpreted in the floras cited above, occur in North and South Carolina, Florida, Alabama, and Louisiana.

Perhaps the nearest relatives of *Capsella* are *Hutchinsia* R. Br., *Hymenolobus* Nutt. ex Torrey & Gray, and *Cochlearia* L. From these it is easily distinguished by its rosulate, nonfleshy basal leaves, its stellate, furcate, and simple trichomes, and its many-seeded, obtriangular-cordate fruits. Several authors have united *Hymenolobus* with *Capsella*, but this is not justified, and the former is more

allied to and perhaps not sufficiently distinct from *Hutchinsia*, which has two- to four- (instead of many-)seeded fruits characteristic of *Hymenolobus*. The direct relationship between *Capsella* and *Neslia* Desv. with *Camelina* Crantz, as proposed by Von Hayek, reflects no more than superficial resemblances.

The remarkable uniformity within a given population of *Capsella Bursa-pastoris* is attributed to extensive inbreeding and particularly to autogamy. Some ecological factors, however, may play an important role in determining the amount of selfing. Hurka, Krauss, Reiner, & Wöhrmann showed that dry and sunny days favor outcrossing and induce the formation of protogynous flowers, while cloudy or rainy days (i.e., low light intensity, high atmospheric humidity, and temperatures above 15°C) lead almost exclusively to selfing. Furthermore, cold weather appears to suppress the formation of normal anthers. Gynomonoecious and gynodioecious plants may be produced early in the season, while functionally perfect flowers are produced in early spring (Knuth), and male-sterile ones may be encountered toward the end of the season (Stace). Numerous species of bees, beetles, butterflies, flies, hoverflies, and thrips have been observed as occasional visitors of the flowers (Knuth).

Self-incompatibility has been reported in forms of *Capsella Bursa-pastoris* known as *C. grandiflora* (Riley, 1932, 1936). Although Riley suggested the presence of three mating groups controlled by two genes (each with two alleles) showing epistasy and dominance, Bateman believed that self-incompatibility in *Capsella* can be better explained as controlled by one locus with at least three alleles showing dominance.

Two chromosomal levels, diploid ($2n = 16$) and tetraploid ($2n = 32$), are known in *Capsella Bursa-pastoris*. Crosses of plants with the same chromosome number always yield fully fertile offspring, regardless of the morphological differences between the parents. On the other hand, crossing diploid and tetraploid plants produces sterile triploids with abortive pollen and shriveled seeds. Such triploid hybrids are widely distributed in nature and have been named *C. × gracilis* Gren. They are said to be derived from *C. Bursa-pastoris* and *C. rubella*. Many authors have considered the last "species" a diploid, but the painstaking work of Svensson indicates that diploid and tetraploid populations in this complex are morphologically indistinguishable, even though the tetraploid tends to have slightly larger sepals, petals, fruits, and seeds. The tetraploid plants flower earlier than the diploid and appear to have wider distribution.

The genetic basis of variation in *Capsella* was studied by Shull (1929), who grew more than half a million individuals and analyzed some 4000 pedigreed lines. He crossed *C. Bursa-pastoris* (obtriangular fruits) with *C. Heegeri* Solms (elliptic fruits) and discovered that the latter is nothing but a double recessive mutant segregating in the second generation at a ratio of approximately 15:1. The mutant was treated earlier as the basis of a new genus, *Solmsiella*.

The embryogeny of *Capsella* has been more thoroughly studied than that of any other crucifer and has been included in numerous textbooks of plant anatomy and embryology as typical of the dicotyledons. The embryogeny is not repeated here, and further details are found in the classic works of Schaffner, Souèges, and Rijven. The ultrastructure, morphogenesis, and growth and de-

velopment of embryos have been thoroughly covered in many papers listed in the references.

Plants of *Capsella* contain high concentrations of allylglucosinolates and small amounts of the alkaloids tyramine and sinapine. The fatty-acid composition of the diploid "*C. rubella*" and "*C. grandiflora*" is indistinguishable from that of the tetraploid *C. Bursa-pastoris*. Seeds from the temperate regions tend to have a higher oil content than those from colder areas (Mukherjee *et al.*). The genus resembles most members of the Lepidieae in having high concentrations (20–35 percent) of linoleic and linolenic acids and negligible amounts (0.2–0.7 percent) of erucic acid.

An anatomical peculiarity of *Capsella Bursa-pastoris* is the derivation of the interfascicular cambium of the shoot from the starch sheath (Hurka & Büchele). The seed coat of this species is indistinguishable from that of "*C. rubella*" and "*C. grandiflora*" and is composed of palisade cells broader than long and with thickened radial and inner tangential walls, and of epidermal cells with a large, solid column protruding into the lumen from the inner tangential wall (Vaughan & Whitehouse).

A single plant of *Capsella Bursa-pastoris* may produce 5000–90,000 (usually 30,000–60,000) small seeds weighing about 0.1 mg (Hurka & Haase). The mucilaginous epidermis of the seed coat aids in long-distance dispersal by adhering to animals and farming machinery. The seeds may retain viability after passing through the digestive tracts of birds and earthworms. The species shows a remarkably high degree of phenotypic plasticity, and the plant may produce fruits within a few weeks after seed germination. Although seed size is genetically controlled, it is also phenotypically plastic; plants of severely cold climate usually produce larger seeds than those in more favorable areas (Hurka & Benneweg).

Seeds of *Capsella* show pronounced dormancy that can be broken experimentally by cold treatment after imbibition. An increase in nitrate level and a fluctuation in temperature can replace the requirement for stratification and are therefore important in breaking seed dormancy in nature. Cold-treated seeds may fail to germinate unless exposed to light at the soil surface (Popay & Roberts, 1970a, 1970b).

Barber (1978a, 1978b) indicated that the seeds of *Capsella Bursa-pastoris* show protease activity in their mucilaginous sheath and are capable of uptake and incorporation of radioactively labelled amino acids. Seeds attract soil nematodes, protozoans, and bacteria, causing some mortality, and they may even derive some nutrients from them. Barber suggested that these adaptations may supplement the nutrition of the germinating seed but questioned whether the seeds are truly "carnivorous."

Many medicinal properties have been attributed to *Capsella Bursa-pastoris*, and various preparations have been prescribed to treat tumors, nasal and internal bleeding, stomach disorders, irregular menstruation, kidney complaints, dysentery, and dropsy. The plant is also considered antiscorbutic, stimulant, astringent, and diuretic (Caius, Hartwell, Perry). The young rosettes are eaten as a salad and are regarded as an excellent substitute for spinach and a rich source of vitamin C. The plant is sold in some parts of China and India.

Cattle feeding on large quantities of it often produce tainted milk. Finally, in addition to being a troublesome weed, *C. Bursa-pastoris* is a host for several fungi and viruses that attack cruciferous crops.

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